

WHY ARE FEMALE BIRDS OF PREY LARGER THAN MALES?

by

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For every complex problem there is a simple answer and it is wrong.

H. L. Mencken

The males of most birds are larger than the females, but the opposite is true of birds of prey—the hawks and owls of the orders Falconiformes and Strigiformes. In these females are, with few exceptions, larger than males—sometimes markedly so. These two orders are only distantly related, and one may assume that this reversed sexual dimorphism evolved independently in the two orders. Further, in the predatory family Stercorariidae, the skuas and jaegers (hunters), the female is also the larger sex; this family is related to the gulls (Laridae), not to hawks or owls.¹

In all these raptorial birds the claws of the feet are modified into curved, pointed talons, which are employed to seize, kill, or aid in killing the prey upon which they feed. In another somewhat predatory family, the Laniidae or shrikes, the bill is hooked as in raptors, but the claws are not modified into talons. The sizes of the sexes are not reversed in shrikes.

There are hundreds, indeed thousands, of other species of birds ranging from flycatchers and swallows to storks which are also “carnivorous,” and yet in which the male is the larger sex. But these species, with only occasional or rare exceptions, capture inoffensive prey—often insects, snails, and the like. Though predators in the literal sense, unlike the truly rapacious birds of prey, they do not have to subdue, kill, and rend their prey; and they have not evolved the hooked beak and talons—or the fierce disposition that goes with such weaponry.

To analyze in detail the data supporting reversed sexual dimorphism in raptors and the possible explanations for it would require a volume. Here the intention is merely to summarize some of the hypotheses that have been advanced and to evaluate them briefly. Neither have I presented in detail the raw data which may be found in various reference works. It may be noted, however, that there is a need for further quantitative data on size dimorphism in raptors. This is particularly true of weights, which reflect the dimorphism better than do linear measurements, such as wing length. The family Stercorariidae illustrates this point. Linear measurements often show superiority in size of the female in the skuas (*Catharacta*) but not in the smaller jaegers (*Stercorarius*) (see, for example, Ridgway, 1919:681-695). When, however, adequate samples of weights of the three species of jaegers were assembled (Maher, 1974:11-12), it became evident that females are appreciably heavier than males in this genus also. Or, as another example, the wing length of the male American Goshawk (*Accipiter gentilis atricapillus*) averages about 97 percent of that of the female; it weighs a full 20 percent less.

¹ In the frigate-birds (*Fregatidae*) females are larger than males. Since these birds are somewhat predatory, it has been assumed (Amadon, 1959) that this is another example of sexual size reversal in raptorial birds. Perhaps so, but the fact that the same is true of the related fish-eating boobies (*Sulidae*) but not of the cormorants (*Phalacrocoraciidae*) makes it possible, if not likely, that other selective factors are at work in this order (*Pelecaniformes*).

In their analysis of size dimorphism in North American owls Earhart and Johnson (1970) couch the discussion of weight largely in terms of the cube root of that dimension. This converts weight to a statistic comparable with linear measurements, such as wing length. Still, it is worth emphasizing that selection for body size results from the actual weight or mass of the bird. The authors mentioned take this for granted in their discussion of the sexual difference in wing loading that results from dimorphism in size.

Variation in Degree of Dimorphism

Raptors vary greatly from genus to genus and sometimes from species to species in the amount of sexual size dimorphism. Those species that are most rapacious and kill the largest prey relative to their own size have the greatest dimorphism. Examples range from certain eagles, such as the Black and White Hawk-eagle (*Spizastur melanoleucus*), the horned and eagle owls (*Bubo*), and the larger falcons (*Falco*) to small species of *Accipiter* and some small owls. In many of these the male is a full third smaller than his mate, and hence called a "tiercel" by falconers. In a few species of *Accipiter* the male weighs only about half as much as the female.

Birds of prey with the propensity to attack large and at times dangerous prey concomitantly develop the fierce and aggressive disposition necessary for such foraging. In species that take smaller or humbler prey, such as rodents, fish, and lizards, sexual dimorphism is less, but often still substantial. For example, in sea-eagles (*Haliaeetus*), various species of *Buteo*, and others the weight of males may average one-fifth to one-fourth less than that of females. In primarily insect- and snail-eating raptors, or those that are in part scavengers, such as caracaras (*Polyborus*) or some kites (*Milvus*), size dimorphism is usually even less and may be negligible.

The social habits of certain kites may also have ameliorated their aggressiveness and led to an abatement in selection for sexual dimorphism. The same may be true of Eleanor's Falcon (*Falco eleanorae*), which, as Dr. Noel Snyder (in litt.) has pointed out to me, shows remarkably little dimorphism for a bird-eating species. To be sure, the fact that most of the birds it catches are small may be a factor. Social habits and extensive use of insects as food may explain the fact that in the Burrowing Owl (*Athene cunicularia*) males average slightly larger than females.

Another exception is the Secretary-bird (*Sagittarius serpentarius*); it occasionally kills large, venomous snakes, but its claws are blunt, not modified into talons. Though classified with the birds of prey, it may be unrelated to them. Among vultures, which are for the most part entirely carrion eaters, the sexes are of about the same size, or the male may even be a little larger. The claws of vultures are long, coarse, and blunt—no longer talons. The Old World vultures, in particular, are closely related to other birds of prey and presumably derived from them. It is reasonable to assume that as they gradually lost their predatory habits, they also lost their reversed sexual size dimorphism.

The correlation just traced is sometimes evident among the species of a single genus. The Peregrine Falcon (*Falco peregrinus*) preys on birds, including large ones; it has pronounced dimorphism. More or less insectivorous species of the genus, such as the kestrels, are less dimorphic. Bird-eating species of *Accipiter* are highly dimorphic; the amphibian-eating Grey Frog-hawk (*A. soloensis*) of the Orient is less so. Earhart and Johnson (1970:260) found that within a single species, the Screech Owl (*Otus asio*), the chiefly insectivorous subspecies are less dimorphic than ones that take many birds and small mammals. The same may be true of the American Kestrel (*Falco sparverius*) (Storer, 1966:433-434).

Thus, one finds on the whole a remarkably close correlation in birds of prey between degree of rapaciousness and degree of reversed sexual dimorphism.

Why Reversed Dimorphism?

Hypotheses fall into two main categories. The first relates reversed sexual dimorphism to one or another aspect of reproductive behavior. I continue to favor one such hypothesis. But before discussing behavioral explanations, I shall consider and attempt to dispose of the prevailing alternative hypothesis, namely, that dimorphism in raptorial birds is an adaptation to widen the food niche.

That is, if the larger female takes larger prey on the average, and the smaller male takes smaller prey, between them they will utilize a greater diversity of the potentially available food. Such expansion of the food niche might be important during the nesting season, when the pair of raptors is restricted to the general vicinity of the nest and when they have voracious young to feed. It might also be of importance to some species during winter or other periods of possible shortage of food.

At present those who see in the size dimorphism of raptors an adaptation to expand the food niche are in the majority. This may be attributed in part to the current popularity of studies embraced by such terms as "time and energy budgets," "(avian) energetics," "adaptive strategies," and "physiological ecology."

There are certainly birds and mammals in which the sexes differ in size but eat the same thing (e.g., grazers, whether geese or wild cattle). Among predators, however, as would be expected, large individuals tend to kill larger prey than do smaller ones. Large female accipiters take on average larger prey than do the smaller males (Storer, 1966; Brosset, 1973), and the same is true of *Circus* (Schipper, 1973) and doubtless of other highly dimorphic species, such as the larger falcons.

But the fact that a large hawk (or person) eats more and prefers larger bites than a smaller one is not necessarily the reason it is larger.

Reasons for doubting the ecological or niche-expansion explanation of reversed sexual size dimorphism among raptorial birds are the following:

First, as already summarized, the degree of sexual dimorphism in raptors is correlated with the relative size of the prey taken, not with the potential of the food supply for supporting dimorphism. Species that regularly or not infrequently attack and kill birds or mammals as large or larger than themselves have the greatest dimorphism. Such species range in size from sparrow-hawks to big eagles. Species that take humbler prey, even when there would seem to be as great or greater potential for broadening the food niche, are less dimorphic.

Second, the ecological hypothesis fails to explain, at least convincingly, why it is the female that is the larger sex. Some (e.g., Selander, 1966:139) recognize this failure and attribute the initial impetus towards reversal to behavioral factors, but then assume that the dimorphism, because of its extent, must be under ecological control. Others have suggested (Prof. E. Mayr, pers. comm.) that since the male does most or all of the hunting in the first half or three-fourths of the nesting cycle, it is advantageous for it to be the smaller sex because (a) there are more species and individuals of small than of large prey (Elton's "pyramid of numbers"), and so the male can get more food at the time he is doing all the hunting; and (b) smaller prey is more suited to the chicks when they are small.

There are a number of caveats to be entered here. Will a larger number of small prey always add up to a larger biomass, especially when much of the prey has to be transported to the nest? Some buteos feed on insects when away from the nest but carry only vertebrates to the nest; insects are too small to make it worthwhile. Certain species commence nesting when the country is still cold or even snowbound, when the prey animals have not yet brought forth their young, and when smaller rodents are less available. The strongly dimorphic Great Horned Owl (*Bubo virginianus*) in the northern parts of its range begins nesting in late winter when the ground is still covered with snow. Not until weeks later, when the young are well grown and when the female is also hunting, are young prey animals

available. Nor is small prey necessarily more suited to the chicks. The female might find it easier to tear bits of flesh for the young from, say, a rabbit, than from a mouse.

Dr. Ned Johnson (pers. comm.) has suggested to me that following an initial selection for larger size in the female for behavioral reasons, females that paired with smaller, more agile males that were better foragers would leave the most progeny. Skill in aerial food passing in courtship might be part of such selection. This hypothesis is attractive for such species as harriers (*Circus*) or some falcons, but if one considers it in the gamut from small owls to eagles it is less convincing. A raptor that is a little less agile may offset it by catching bigger prey. The larger female does some effective hunting after the young are well grown, as well as hunting for herself during the nonbreeding season.

Reynolds (1972) concluded that if dimorphism is an adaptation to broaden the food niche, then it will be greatest in bird-catching species, such as the Sharp-shinned Hawk (*Accipiter striatus*), in which the size of the predator approximates that of the agile prey. But surely the vast majority of the birds caught by this species and by related ones, such as the European Sparrow-hawk (*A. nisus*), weigh no more than a third or perhaps half as much as the hawk. The argument is perhaps undercut to some extent by Reynolds's evidence that the larger female, when she does commence hunting later in the cycle, is effective because her size enables her to take a greater size range of prey. And as with other ecological hypotheses, the pronounced dimorphism in many species that catch few birds remains unexplained. Weight data (Glutz, Bauer, and Bezzel, 1971:173,642) indicate, for example, that in the European race of the Golden Eagle (*Aquila chrysaetos*) and even in the White-tailed Sea-eagle (*Haliaeetus albicilla*) the average weight of the males is a full 25 percent less than that of the females.

Third, a survey of the animal kingdom suggests that sexual dimorphism in size is usually correlated with mating behavior (Amadon, 1959). In general, males are more aggressive than females; they compete for mates. Larger and stronger males have an advantage in perpetuating their genes. This distinction may be less apparent in birds than in mammals, but it exists. Even in the occasional insect in which males contest physically for mates, selection has produced larger size in that sex (Beebe, 1947). The increased dimorphism often found in polygynous or promiscuous species, such as some of the larger grouse (*Tetraonidae*) or pheasants (*Phasianidae*) or bustards (*Otididae*), further illustrates the point. In highly polygynous seals (Phocidae), such as the elephant-seals (*Mirounga*) or northern fur seal (*Callorhinus*), two genera that are not closely related, males weigh several times as much as the females. In these polygynous birds and mammals, males are to a degree expendable; only a few are needed for fertilization. Hence, sexual dimorphism can proceed further than in monogamous species. In the latter, among seals as well as birds, dimorphism is much less. An ecologist who saw in the enormous dimorphism of some of the polygynous seals an adaptation to broaden the food niche would surely be mistaken!

When the parental-care role is reversed, as in phalaropes (*Phalaropidae*) or button-quail (*Turnicidae*), and the males incubate and care for the chicks while the females compete for mates, it is the females that are the larger, and, when there is a distinction, the more brightly colored sex. Female button-quail are so pugnacious that they are pitted like miniature gamecocks. The reversed sexual dimorphism of raptors is not associated with reversed roles in parental care. The instances above are merely cited to further illustrate the responsiveness of size to selection by reproductive behavior.

The skuas and jaegers (*Stercorariidae*) seem to confirm this observation. In the related gulls (*Laridae*) males are larger than females. Yet, when the skuas became even more predatory than gulls, and, especially, one supposes, when they developed small, curved "talons" that could pose a threat to the female in pairing and territorial encounters, selection came to favor larger size in the female. Perdeck (1960), who studied nesting behavior in

the Great Skua (*Catharacta skua*), is quoted on this point below.

Though probably without immediate relevance to the situation in birds of prey, one may cite Jehl's (1970) study of dimorphism in certain Scolopacidae. In the Stilt Sandpiper (*Micropalama himantopus*) and the Least Sandpiper (*Erolia minutilla*) he found that individually small males and large females pair first and are most successful in nesting. Again, if he is correct, the dimorphism has its basis in reproductive behavior, not in ecology. The fact that the female is the larger sex in these shorebirds is unrelated to the situation in raptors, but reflects the trend towards reversal of parental care in shorebirds that has become complete in such groups as the phalaropes.

Thus there is varied evidence that sexual size dimorphism among higher animals is commonly the result of patterns of mating behavior. The burden of proof is upon those who suggest that the same is not true of raptorial birds.

Fourth, there are doubts as to the theoretical basis of the ecological or niche-expansion theory. One assumes that intraspecific competition among birds is regulated by such adaptations as territory, peck order, delayed reproduction, cannibalism, and the like. Such competition is often density dependent and will not lead to extinction. Interspecific competition, on the other hand, may pose a direct threat to survival, and thousands of species have doubtless succumbed to it—sometimes, to be sure, when also beset by environmental changes. Because the environment does change seasonally, annually, and over longer periods, successful species evolve various safety factors. One may be a body size that is not rigidly limited by food or environment. Such ecological amplitude may be especially necessary in top-level predators whose food supply is often more uncertain and fluctuating than that of the grass eaters which sustain them.

Hence in species in which mating behavior makes sexual dimorphism in size advantageous (and this includes most birds and mammals), the ecological niche, one supposes, is often or perhaps usually molded by selection to accommodate the size variation and not vice versa. Such modifications may entail increased size of territory, heightened interspecific aggression, etc. Some species, to be sure, adjust with difficulty; perhaps this is why certain raptors, such as the Ayres' Hawk-eagle (*Hieraetus dubius*) or the Taita Falcon (*Falco fasciinuca*), are so rare. Others become extinct.

To state this the other way around, would not interspecific competition be least when a species is clustered around its optimal competitive size, without sexual-size dimorphism? If so, the widespread occurrence of dimorphism among higher animals may be regarded as a behavioral necessity. To what extent theoreticians have dealt with such questions I do not know. Schoener's contributions (e.g., 1968, 1969a, 1969b) seem to deal with rather complex situations, and his equations have so many variables as to render conclusions from them tentative.

Even if interspecific competition is disregarded, sexual differentiation in food or foraging niche may not be advantageous in the long run. If the food supply changes, there are two things that can go wrong, not one. It may be more difficult for such a dimorphic species to adjust to changing food resources or levels of interspecific competition.

Thus when it is demonstrated that the smaller male, as might be expected, requires fewer calories than does the female (Mosher and Matray, 1973) of the Broad-winged Hawk (*Buteo platypterus*), one does not need to accept the suggestion that the smaller size of the male reflects direct selection to lessen caloric requirements. Why would such selection have affected the male only? Why do species become larger in the first place if caloric requirements are of such crucial importance? This, of course, is not to deny the importance of such studies in determining physiological parameters.

The fossil record contains many examples (and in diverse groups!) of a trend towards increasing size. Larger individuals may secure more mates, or they may be able to shoulder companions away from food or other necessities (Simpson, 1944:86). The trend towards larger size is a general one, and the blue whale (*Balaenoptera musculus*), a plankton eater, has become the largest known animal of all time. In thousands of diverse animals, and perhaps one might include plants, size has not been so rigidly controlled by food or other environmental factors as to preclude gradual change. Often it has continued to change over vast periods of time.

To be sure, a number of examples of sexual dimorphism in birds apparently represent adaptations to expand the available food resources (summarized by Selander, 1966). These usually relate to the primary food-gathering organ, the bill, rather than to general size, and the species concerned are chiefly inhabitants of depauperate islands where interspecific competition will usually be less than on continents. Even so, the evidence that the observed sexual differences in foraging are the *cause* of the dimorphism is circumstantial. Perhaps the species-poor habitats merely provide more scope for divergence resulting from social or sexual behavior (dominance, peck order, mating systems, facilitation of sex recognition, etc.).

I do not, of course, wish to deny that food availability or lack of availability may sometimes have had something to do with degree of dimorphism in raptorial birds. Earhart and Johnson (1970) found some races of *Bubo virginianus* to be slightly more dimorphic than others; this may reflect some environmental influence, but it could be a result of mere chance.

Behavioral Explanations

It will be clear from what has preceded that I continue (Brown and Amadon, 1968:26-28) to think that the explanation for the reversed sexual size dimorphism of raptorial birds is to be sought in the relationships of the male and female at the time of pair formation and perhaps throughout the reproductive period. Before discussing this, we may dispose of hypotheses based on other aspects of behavior.

First, it has been suggested that male birds of prey, lacking "maternal" instincts and accustomed to killing small animals, may pose a threat to the life of nestlings. Selection might then favor larger size in the female so that she can prevent any such attempts by the male. Perhaps such reflections were influenced by knowledge of certain mammals, such as cats and bears, in which the males are, in fact, a threat to the young. There is now ample evidence that even in raptors with pronounced sexual dimorphism the male often incubates to some extent and may even have a brood patch. He sometimes feeds the chicks and certainly poses no threat to them.

A second hypothesis suggests that selection has favored larger size in the female raptor, the better to enable her to protect the nest and its contents from predators of other species. This suggestion is more difficult to disprove, but I do not think it will pass muster. It is true that the female spends more time at the nest than the male, but why, if nest defense explains the larger size of female raptors, should the dimorphism be greatest in fierce species that catch relatively large prey? It might be argued that because they are fiercer, they defend the nest more vigorously; therefore selection for increased size is more severe. This is rather tenuous reasoning. To be sure, two fierce species, the Great Horned Owl and the Goshawk, are the North American raptors that most often attack humans climbing to the nest. But it is also true that many raptors with rather pronounced dimorphism, such as the two species of North American eagles, are lackadaisical about nest defense, at least insofar as humans are concerned.

Scattered evidence indicates that males do participate in nest defense. In Great Horned Owls both members of a pair sometimes attack an intruder, striking alternate blows. Both members of a pair of Ferruginous Hawks (*Buteo regalis*) attacked a coyote that was unsuspectingly approaching their hillside nest (Angell, 1969). A male Merlin (*Falco columbarius*) sometimes appears, screaming in protest, when an intruder is still far from the nest. When raptors nest or attempt to nest in captivity, both members of the pair may become very aggressive towards man or any intruder, as was true of an observed pair of Harpy Eagles (*Harpia harpyja*) (Dr. William G. Conway, pers. comm.).

Nest defense is a two-edged sword: better to flee and live to nest another day than to be killed by a nest predator. Golden Eagles occasionally bring Great Horned Owls to their young as food; perhaps these were owls that defended their own nests too vigorously! The species of raptors found in any particular area usually exhibit wide divergence in dimorphism; it seems unlikely that nest defense is more important to some of them than to others.

Thirdly, the suggestion is made that contests between male raptors are primarily brilliant aerial maneuvers and that smaller size in the male, far from being a handicap, is an asset. This is an attractive idea as applied to a dashing falcon, but not for a big eagle or a horned owl. Further, Cade (1960) found that large falcons do in fact make bodily contact in aerial encounters and that sheer physical prowess is the deciding factor.

We turn, finally, to the hypothesis that reversed sexual dimorphism is the result of reproductive interactions between the sexes. Pair formation may prove to be the decisive phase.

In highly dimorphic birds as regards color—many pheasants, for example—sex recognition may be innate; but in the numerous species in which the sexes are externally alike, this includes most raptors, initial pair formation is often—as the late R. C. Murphy once put it—a matter of trial and error. Typically, the male takes up a territory and, by displays and vocalizations, warns off other males and attracts females. He is hostile to *any* approaching conspecific, treating it as a potential rival and buffeting it or otherwise seeking to chase it away. If the approaching bird is a female prepared to mate, she behaves submissively, refuses to be repelled, or thereafter returns and a pair is formed (Lack, 1940).

If this is the sequence in raptors, and many more observations are needed, may not the female be in actual peril from a male armed with talons and (judging from birds in general) innately more aggressive than she? Indeed, the male might first appraise an approaching bird of his own or smaller size as potential prey! In such species selection would, one assumes, have favored females that were as large as, or eventually larger than, the male so that despite their somewhat more submissive or passive nature at the time of pairing, they would not be intimidated or imperiled by the male. This would be especially true of species that unhesitatingly attack birds as large or larger than themselves. It is in such species, as has been already emphasized, that the superior size of the female is usually most pronounced.

If such is the case, one might ask why sexual dimorphism is substantial in some buteos, fish eagles, and the like, which subsist on rather humble prey. These raptors are, however, all armed with dangerous talons, and most of them do at times attack large birds or mammals. A few examples will be given. A Red-tailed Hawk (*Buteo jamaicensis*) when flushed, flew off carrying the body of one of its own species which it had apparently killed and was eating (Clevenger and Roest, 1974). A White Hawk (*Leucopternis albicollis*), a species that normally feeds on small snakes and the like, killed a tinamou (*Tinamus major*), a bird that would weigh more than the hawk (Lamm, 1974). The American Kestrel occasionally tackles a bird as heavy as itself. The Bald Eagle (*Haliaeetus leucocephalus*), though partial to fish, not

infrequently pursues and kills large birds; some individual eagles do so habitually. Further, *Accipiter* and *Falco*, instructive though they may be, do not provide all the necessary evidence. For example, speculation about the correlation of increased sexual dimorphism in color and reduced dimorphism in size in *Falco sparverius* cannot ignore other genera (or even other species of kestrels) in which no such color dimorphism exists.

Careful observations of both wild and captive raptors are needed. The behavior of captive birds may be significant but must be interpreted with caution. In the wild, for example, courtship or pairing flights may cover miles of terrain. Willoughby and Cade (1964) in an attempt to study dominance in relation to size dimorphism, paired a male of the northern race of *Falco sparverius* with the female of the smaller southern subspecies, thereby forming a pair of about the same size. Behavior did not seem abnormal, but this is a species of rather moderate dimorphism.

It might be argued that things have swung too far. In courtship feeding in the Peregrine Falcon the male sometimes appears terrified of the larger female; she snatches the prey from his grasp as he speeds by. Where attempts have been made to breed various species of *Accipiter* in captivity, the male, lacking sufficient room to flee, is sometimes killed by the female. Nonetheless, under natural conditions, one assumes that the existing degree of dimorphism in each species is the optimum under existing selection pressures.

As noted earlier, Perdeck (1960:129) in his study of *Catharacta skua* came to the conclusion set forth above as to the reason for reversed sexual dimorphism. If he was correct, the same could be true of hawks and owls. He summarized as follows (slightly paraphrased):

Perhaps the piratical and sometimes predatory habits of the skua have something to do with the reversed male-female size ratio, as compared with the gulls. A predatory bird needs a high aggressiveness towards other birds that may not only be its equal in size but also be of the same general appearance (skuas prey upon gulls). But this extreme aggressiveness is a drawback in pair formation and mating. A male has to perform the most 'aggressive' part of the mating. For the male to be in general more aggressive than the female has, therefore, survival value. But he must, of course, not be too aggressive! The chance of this occurring is greater in a species that, because of its feeding habits, requires an extra 'dose' of aggressiveness. For such a species a reduction in the size of the male relative to that of the female may have survival value.

In passing, it may be noted that sex recognition in predatory mammals is based on other cues, probably initially olfactory ones, and there is no reversed dimorphism.

To attribute such a fundamental character as sexual dimorphism in size in raptors to a selective pressure that operates only during the relatively brief period of pair formation and mating may seem unrealistic. Yet many birds (and mammals) are encumbered throughout adult life with "ornaments" used only at that season (for example peacocks [*Pavo*]). At the same time it is possible that the reversed dimorphism of raptors may enhance reproductive success throughout the entire nesting cycle. Cade (1960) wrote as follows:

A reproductively successful pair bond can result only when the female falcon is clearly dominant to the male . . . and when the male makes a biologically adequate adjustment to his subordinate role in the pairing situation. . . . Female dominance appears to function in some as yet unknown way in holding the male to his role as food provider for the female and the young. . . . On the average, females that mate with males smaller than themselves were able [one supposes] to maintain better dominance relations, and more progeny of such pairs survived. . . . Even in Kestrels, in

which the dimorphism is less, the females "assert a vigorous dominance over their mates."

In the Goshawk, Schnell (1958:385) found that the female had a special cry with which she "dismissed" her mate; and she did not begin feeding the chicks until after he had left the vicinity of the nest. Kemp and Kemp (1975) observed a female Ovampo Sparrow-hawk (*Accipiter ovampensis*) threaten her mate when he remained at the nest after she had finished eating a prey item the male had brought. The male then left immediately. But there are hundreds of species of birds in which one sex, usually the female, assumes the entire duties of parental care without stimulus or assistance from the mate. There are a few observations of male hawks that continued to feed the chicks after the death of the female, and there is no real evidence that physical (or sexual) dominance by the larger female has anything to do with the fact that her mate hunts for her and for the chicks.

How may one demonstrate conclusively whether behavioral or ecological factors or both led to reversed sexual dimorphism in raptorial birds? Comparison of the degree of dimorphism with the opportunities for ecological expansion might provide clues, e.g. comparison of the dimorphism and food resources of the subspecies of *Buteo jamaicensis* on the tiny island of Socorro off the Mexican coast with those of one of the mainland subspecies. Mating and parental behavior may be observed both in the wild and among the raptors that are being bred with greater success in captivity. The data acquired may prove difficult to interpret at least initially, but will also be valuable for other purposes.

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Summary

In most birds of prey, including such unrelated ones as hawks (Falconiformes), owls (Strigiformes), and skuas (Stercorariidae, Charadriiformes), females are larger than males, sometimes substantially so. This reversed sexual size dimorphism in raptors is greatest in species that pursue, kill, and rend large, active prey; less in those that kill small rodents or insects; and absent or virtually so in vultures. In some species it has been shown, as would be expected, that the larger females catch on the average larger prey than the smaller males. Some ecologists conclude from this that the dimorphism is an adaptation to increase the total size range of prey available to a raptorial species. This hypothesis does not explain why the dimorphism is greatest in fierce species that kill large birds and mammals, why in some dimorphic species the sexes apparently take food of the same size, or why it is the female that is the larger sex, although an attempt has been made to correlate the last point mentioned with ecology.

Furthermore, in higher vertebrates in general, sexual dimorphism in size is correlated with mating behavior, not with foraging ecology; it is usually a result of competition by males for mates. When it is the females that compete for mates, then that sex is the larger. Although female raptors do not compete for mates, they are larger than the males; the explanation is probably still to be found in mating behavior. Raptors have become unusually aggressive birds, presumably because they hunt and kill active prey at some risk of injury to themselves. Furthermore the male, as in birds in general, may be expected to be the more aggressive sex, at least at the time of mating and pair formation. Armed as he is with formidable beak and talons, he would pose a threat to the physical well-being of the female during pair formation, which in birds involves aggression by the male during its earlier stages. To offset this, selection would favor greater physical prowess in the female, and hence that sex has become the larger one, especially in the most aggressive species.

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HARRIS' HAWK KILLS EGRET

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The Harris' Hawk (*Parabuteo unicinctus*), though it captures many small animals and is even said to take carrion, at times tackles larger prey without hesitation, both in the wild and when trained for hunting, as the following experience illustrates. On the morning of January 25, 1975, I was photographing in a swampy area along a road in San Luis Potosi, Mexico. A Harris' Hawk flew in, swooped on a lone nearby Snowy Egret (*Egretta thula*), and carried the squawking heron about one hundred yards to a low stub. When I approached, the hawk carried its prey about fifty yards further, landing in a palm tree and dropping the egret, still alive, at its base. Six other snowies flew around the victim excitedly, and then a Common Egret (*Casmerodius albus*) flew in and lit nearby for a couple of minutes. After ten minutes the hawk dropped down, seized the egret which was still able to squawk once or twice more, and laboriously carried it off behind a screen of trees, where the hawk apparently fed. A quarter of an hour later the hawk, unencumbered, returned to its perch in the palm. Probably the egret weighed about half as much as the hawk.